

TROPICAL RAIN FORESTS



Why They
Have So Many
Species, And How
We May Lose
This Biodiversity
Without Cutting
A Single Tree

by Louise H. Emmons

Nineteen years ago, as a graduate student in Gabon, Africa, I became addicted to tropical rain forests. The fascination of the rain forest lies in its stunning complexity.

You can stand anywhere and be surrounded by hundreds of organisms that are all "doing something," going about their living in countless interactions—ants carrying leaves, birds dancing, bats singing, giant blue wasps wrestling with giant tarantulas, caterpillars pretending they are bird droppings, and so on.

I began a career of trying to understand the processes that go on in such forests. Starting in Gabon and continuing later in South America, I learned just how rich in species the richest terrestrial ecosystems are; how some of the organisms within them interact to create and maintain that diversity; and how man may already be changing the entire plant structure of "intact" rain forests without felling a single tree.

My graduate research was on squirrels, and what hooked me was the number of species. A North American forest has one to three squirrels. There were nine of them in that Gabon forest. How do they all manage to live together in one forest, I wanted to know?

What I found out can be summarized briefly: each of the nine species is a different size; three have specialized diets or habitats, which leaves six species that feed on nuts, fruits, and insects, and so potentially compete for food. A closer look showed that three of the six—a large, a medium, and a small one—live in the forest canopy and never come to the ground. The largest, "giant" squirrel feeds mainly on very large, hard nuts, and the smaller ones eat smaller fruits and nuts. The other three species—again a large, medium, and small one—live on the ground and eat fruits and nuts of the same species as their canopy neighbors, but only after they fall to the ground.

In Gabon, the forest is evergreen and not very seasonal; fruit can be found on the trees throughout the year. But any one species of tree produces fruit for only a small part of the year. To support three squirrel species in the canopy (and eight monkeys, eight fruit-bats, etc.), a forest must have a great many species of trees and lianas, each producing fruit in its own rhythm. A variety of sizes of fruit can support different sizes of squirrels; and these fruits, when they fall, feed a whole set of other species on the ground. By contrast, in a temperate forest, fruit is produced in the summer, and the squirrels that feed in the canopy in spring and summer must come to the ground in fall and winter. There are no ecological niches for two separate sets of similar squirrels. Nor



do our temperate forests provide a large array of fruits. The smallest tree squirrel (red squirrel) is able to feed on the largest, hardest nuts—black walnuts and butternuts—which are also the food for the larger gray squirrels.

The nine squirrels of the African rain forest are there, then, because of the enormous number of species of trees and lianas, in a climate that makes fruit available year-round. As I went on to learn, the squirrels provide a clue to some interactions that help explain the biodiversity of the rain forest.

What do we mean when we say that a tropical rain forest is rich in species? Al Gentry of the Missouri Botanical Garden has been working in the tropics for many years, counting the tree and liana species. Recently he reported the richest site found

thus far in the world: near Iquitos, Peru, in the lowland Amazon basin rain forest, a one-hectare plot—about 2.5 acres—had the incredible number of 283 species of trees over 10 cm (4 inches) in diameter. There were 580 trees of this size in the plot, so that on average there were only two individual trees per species. In the first 65 individual trees that Al sampled there were 58 species! As he put it, “It is hard to imagine a more diverse forest.”

Worldwide, tropical rain forests seem to have from about 90 to 283 large tree species per hectare. Even in the “poorest” tropical rain forests, there are an average of only about five individual trees per species in a hectare (although some species have many more). By comparison, the richest woodlands in the United States have about 20 species over 10 cm diameter per hectare, and an average of about 30

A tropical rain forest that is rich in tree species may have very few individuals per species. The fewer individuals there are, the more likely the species would become locally extinct, were not nature to provide ways to help ensure successful reproduction.



Left: Bats like the Indian fruit bat are among the best seed-dispersers, because they tend to carry fruits away from the tree and later spit out the seeds.



Top right: The gray squirrel is the most familiar of the two or three species in most North American forests. In a tropical rain forest, a year supply of fruits and nuts can support as many as nine squirrel species.



Bottom right: Fruits are the food of choice for many rain-forest mammals. Despite the large amounts of green leaves, few mammal species have become adapted to eat them.

individuals per species. Most temperate forests are much poorer than this, however. A tropical dry forest has an intermediate number, with about half as many tree species as a rain forest.

A look at the mammals in these forests reveals a similar difference. A lowland hardwood forest in Virginia has about 35 species of forest mammals, while a single African rain-forest area in Gabon, studied for many years by a group of French ecologists and myself, had 126. There is no complete list of mammals for any of the richest New World rain forests, but we think we could expect to find about 150 species at individual sites in Ecuador or Peru, where the richest areas are most likely to occur. Thus tropical forests have three to four times as many mammal species as temperate ones (figure 1).

The picture for birds is similar: about 40 species live in a rich temperate forest in the southeastern United States, while about 550 have been found at single lowland rain-forest sites in the Amazon basin of Peru. The difference is approximately the same as for trees, about tenfold (figure 2).

If we look a little more closely at the kinds of trees, birds, and mammals in rain forests, some patterns start to emerge. For the trees, we can again turn to studies by Al Gentry, who asked a simple question: As you go from a place with relatively few tree species, say a tropical dry forest, to a place with many, such as a very wet tropical rain forest, what kinds of trees do you "add on" to the community? His startling results (see the pie diagrams) showed that the more species of large trees (over 10 cm diameter) there are in a forest, the more of them depend on birds and mammals to disperse their seeds. In the dry forest, about 64 percent of the trees have bird- or mammal-dispersed seeds, and 36 percent rely on the elements of wind, water, and sun; but in the wettest, most species-rich rain forest, fully 94 percent of the trees have seeds that are dispersed by animals! As tropical rain forests get richer in species, more and more of the trees depend on animals to take their seeds to places favorable for growth (figure 3).

We can ask a similar question about the birds and mammals that are "added on" as you move from a temperate or dry tropical forest to a wet tropical one. Our mammal studies in Gabon showed that virtually all the "extra" mammals in a tropical rain forest were either fruit-eating (56 species) or insect-eating (47 species), with frugivorous mammals accounting for by far the largest part of the increase (there are only 6 fruit-eating mammals in a Virginia forest).

John Terborgh has compared the differences between the food habits of forest birds in a rich temperate forest containing 40 species and a rain

Figure 1

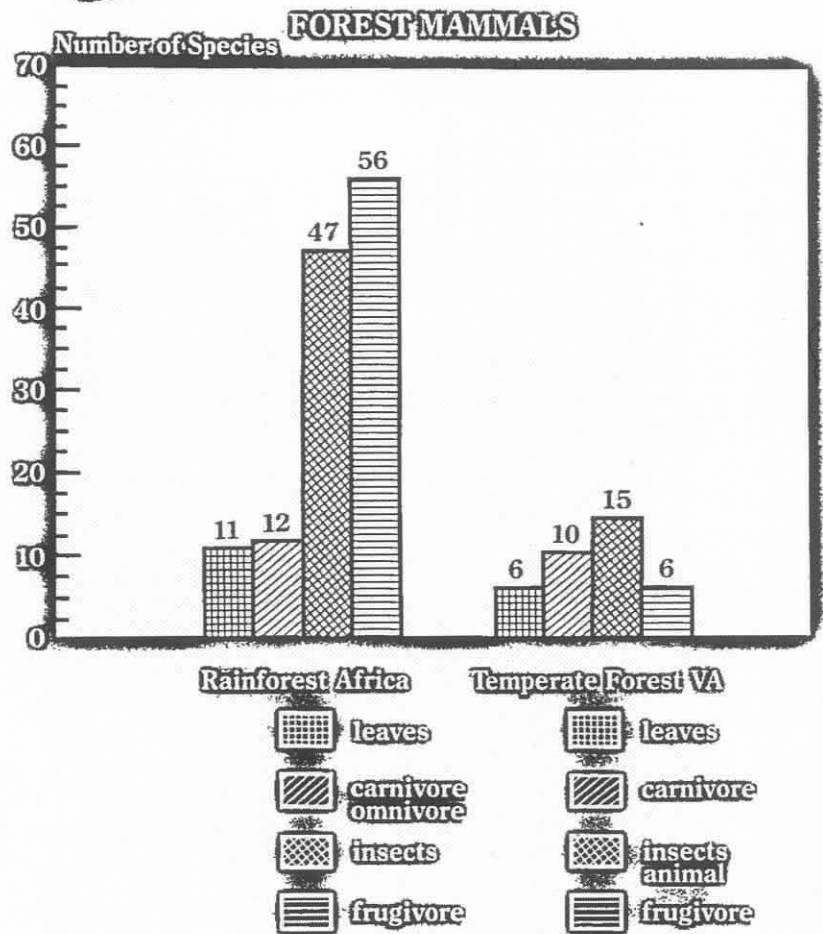
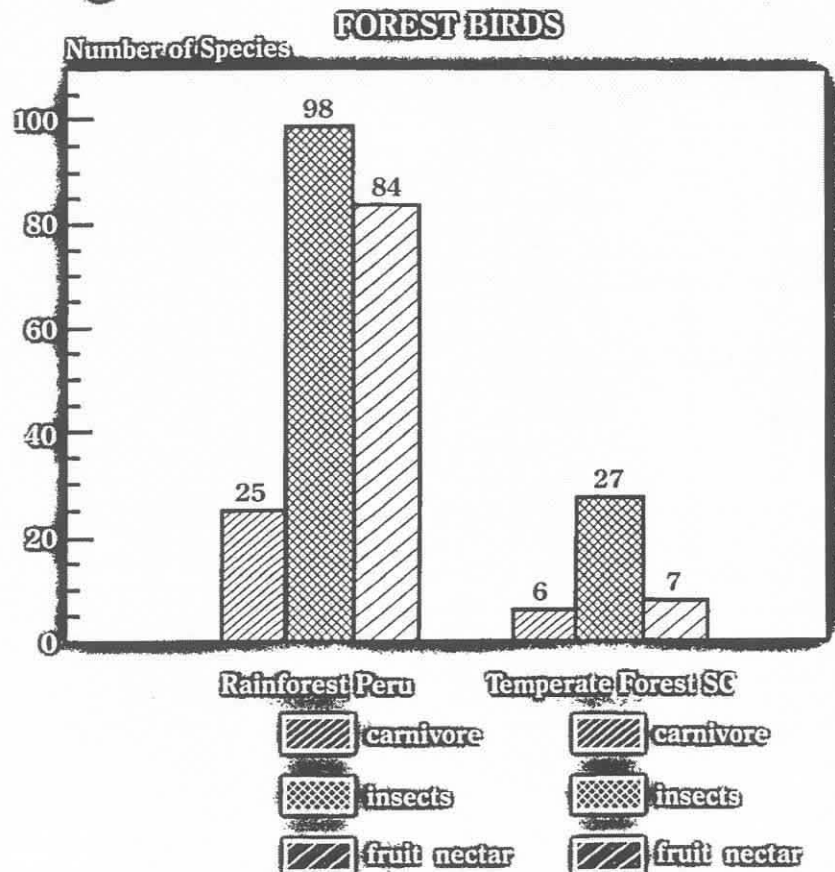
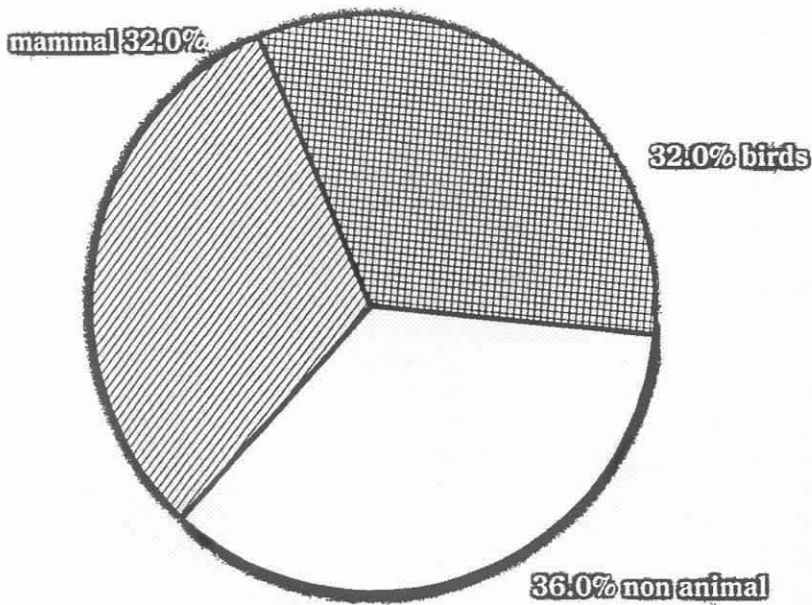


Figure 2



A. TROPICAL DRY FOREST



B. TROPICAL MOIST FOREST (BGI)

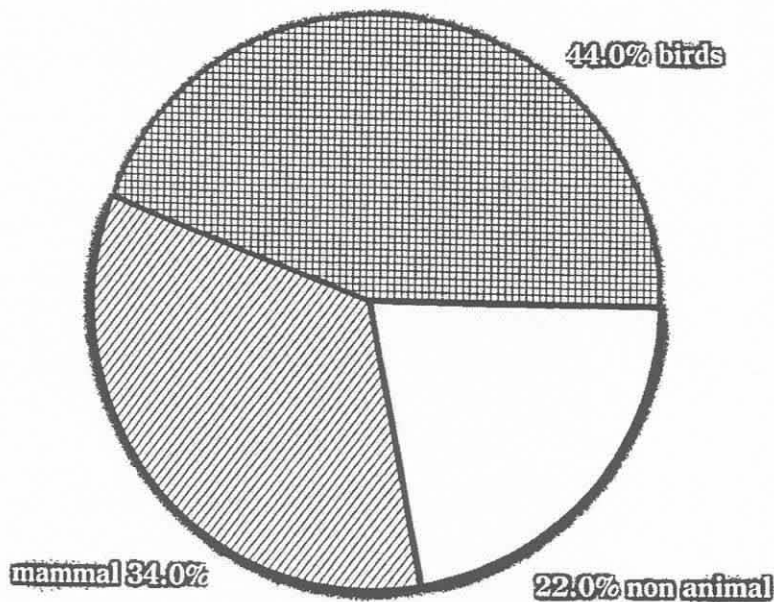


Figure 3

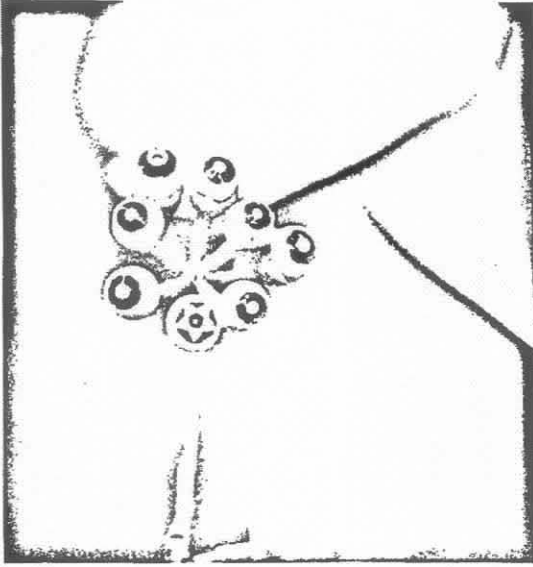
forest with 207 species. Once again, the greatest difference was in the number of birds that include fruit and nectar in their diets—7 temperate-forest birds vs. 84 rain-forest birds, with a smaller but still significant difference in insectivores, 27 vs. 98.

The relationship between the bits of information above now becomes clearer: rain forests are amazingly rich in tree species, but not just any trees—especially trees with fruits that are eaten and whose seeds are dispersed by birds and mammals. Rain forests are also rich in birds and mammals, but not just any birds and mammals—especially those that eat fruits. The biodiversity of each is tied up with that of the others. The enormous number of vertebrates appears to be founded on the number of plant species and the year-round production of food resources.

But what about the plant species? Why are there so many in a tropical rain forest? Scientists have not yet agreed on an answer, though there is a wealth of conjecture. Skirting the question, we can still wonder, how do all these tree species manage to survive when there are so few individuals in any patch of forest? How do they reproduce? One of the answers points to a hidden threat to rain-forest conservation.

If a rich tropical rain forest virtually made up of rare species is to maintain its local biodiversity, each individual tree must succeed in leaving offspring. Much recent research has suggested that dispersal of seeds away from the parent tree greatly improves the chances that a seedling will be able to grow and survive. Seeds and tender young seedlings are among the richest foods available for forest animals, and the high diversity of organisms in a rain forest means there are large numbers of hungry animals searching for seeds and browse. These animals, from mice to weevils, quickly find the fruits and seeds that fall around the base of a fruiting tree. Likewise, pathogens such as fungi and soil nematodes soon accumulate where seeds or seedlings of one species are concentrated, and spread from one seed or seedling to the next. Seeds and their resulting seedlings moved away from such concentrations have a much better chance of escaping discovery by destructive organisms. The other major benefit of dispersal is that seeds are spread over a wide variety of places with different conditions, so that some seeds are more likely to fall in the best places for growth, such as a pocket of better soil on a termite mound, or where a dead tree has created a sunlit gap.

Thus, the birds and mammals that eat fruits and disperse seeds may be the factor that enables seeds to be placed in good positions to grow and succeed. It is certainly no accident that about 80 to 95 percent of



the tree species in tropical rain forests have bird- and mammal-dispersed fruits. The birds and mammals that do this job are vital to maintaining the numbers of species of trees, which, as we have seen, allow the high numbers of birds and mammals to live there in the first place.

Many species of rain-forest trees, especially those whose seedlings become established in the dark forest understory, have large seeds that carry a large energy supply, enough to enable the seedling to grow and put out leaves without much energy from the sun. These fruits and seeds are often so big that only quite large birds or mammals are able to swallow or carry them. In one of our studies in Gabon, monkeys were dispersers for 67 percent of the fruits eaten by animals in the study area.

The seed-dispersing animals most important for the large canopy trees and lianas—the large monkeys and large birds—are the first species to disappear through human subsistence hunting. These, along with elephants, have already been drastically reduced in numbers or completely eliminated by human hunters over vast areas of forest in Africa. The situation in the New World tropics is comparable. There, monkeys, trumpeters, toucans, curassows, guans, fruit crows, agoutis, acouchys, and bats are major dispersers for canopy trees. The first five are hunted intensively for meat, and are now scarce or absent in great tracts of neotropical forest.

For the most part foresters have overlooked the subject of the dependence of plant biodiversity on seed-dispersing mammals. A decade ago, however, D.-Y. Alexandre published a paper on the importance of elephants to forest trees in the Ivory Coast. He found 37 tree species whose seeds were being dis-

Left: A wide variety of rain-forest plants, each bearing fruit at different times of the year, provides food for a correspondingly wide variety of fruit- and seed-eating animals.

Right: The juvenile capuchin, photographed in Peru's Manu Park, would be among the first animals to be hunted out in a less protected area.



Rhamphastos citreolourmas, like other toucans, is a fruit-eater. The birds snap off the fruit with their long bills and gulp it down whole by tossing back their heads.

persed by elephants; of these, only 7 species had alternative dispersers (monkeys and birds). In a plot inhabited by elephants, he found that out of 201 individual trees, 83 were "elephant-dispersed" species. In a forest where man had eliminated elephants a century ago, there did not appear to be many juvenile trees of most elephant-dispersed species, and two major species had no offspring at all. (One of these two, as it

happens, is the single most important species for the two largest squirrels I studied in Gabon—one eats the nuts in the canopy, the other on the ground.)

Once they are empty of large monkeys, large hornbills, large turacos, large toucans, trumpeters, guans, curassows, and elephants, those stunningly rich rain forests can be expected gradually to lose species of trees, lianas, and other plants. Large-animal-dispersed species will be replaced by wind-dispersed ones; species whose seedlings grow in the shaded understory will not succeed, and there will be fewer, more common species in a plot. And when the forests become poorer in plant species, mammal and bird species will also decline. All the complex, interconnected chains will gradually degrade and degenerate, the lost species probably never to return.

Who would have thought that when the elephants disappear from the African rain forest, thirty major tree species could go with them, as well as the two giant squirrels that live on seeds of these species, and who can tell what else? Or that for lack of a few species of monkeys, the whole structure and nature of tropical rain forests as we know them now could change?

The goal of ecosystem conservation should be to try to foresee and prevent such changes. Hunting for meat needs to be managed for sustainable yield. Large monkeys and birds should be monitored carefully, and perhaps not hunted at all. The forest with the most fruits will produce the most peccaries, pacas, deer, or duikers, but few hunters realize that it is the monkey that may be keeping those fruit trees there.

When forests are exploited for timber, foresters know that strips of forest must be left for seed trees, but few may realize that these strips are just as important for the animals that live in them, and that forested corridors are necessary so that animals can get to them. It is often said that once a large area of the rain forest has been cut, it never grows back. One of the reasons may be that the cycles of reproduction that require animals both to pollinate flowers and disperse seeds have been fatally disrupted.

We must work hard to understand the processes that make forests diverse and the measures necessary to keep them that way. As we have seen, deforestation is not the only threat to rain-forest diversity.

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